THE FLORISTIC COMPOSITION OF BRITISH UPLAND VEGETATION IN RELATION TO GRAZING

by D. Welch Institute of Terrestrial Ecology, Banchory Research Station, Hill of Brathens, Glassel, Banchory, Kincardineshire.

SUMMARY

Opinions concerning the effects of grazing on floristic composition in the British uplands are briefly outlined. Grazing is considered the major factor controlling whether a site will bear woodland, dwarf-shrub heath or monocotyledonous grassy vegetation. Successions within the grassland type are discussed, particularly those involving the less palatable species *Juncus squarrosus*, *Molinia*, and *Nardus*. These plants are not thought likely to spread widely into Agrosto-Festucetum. Grazing is held to have impoverished the flora in average upland vegetation. But the total flora is little affected because ungrazed refuges always exist for the species which cannot withstand defoliation, and in small areas diversity is increased because more species can occur when plants are kept short.

Introduction

Much has been written about grazing in the British uplands, but the complex biological processes involved are by no means fully understood, so often statements on grazing have tended to be more reflections of personal opinion than proven scientific facts. This accounts in part for the continuing controversy on whether grazing is 'harmful' or 'beneficial', and whether the British uplands are under or over-grazed. When pronouncements are made on such issues, circumstances and standpoint should be made clear (Welch, 1969). Too often this has not occurred, and too often authors have accepted as fact judgements which were perfectly valid as initial appraisal, but which should not rank equal to the findings of systematic study. There has also been failure to distinguish between grazing per se, and the customary aggregate of management practices associated with it.

The attack on free-range grazing, particularly by sheep, was led by Darling (1955) and Pearsall (1950). Their ideas proved persuasive, and have been amplified by many subsequent writers including Coppock & Coleman (1970), Hart (1968), McVean & Lockie (1969) and Tivy (1973). The tenor of their comments is exemplified by a quotation from Hart. "In general, sheep, by their close and selective grazing . . . gradually bring about the suppression of all but the coarsest grasses, weeds, heathers and sedges; while their close treading leads to compaction of the soil. This causes loss of aeration and absorptive capacity, and thus inhibits the circulation of soil minerals. Hence the sad appearance of hundreds of square miles of upland pastures, in which the greyish and brownish tints of the coarse grasses are relieved only by sparse flowers, . . . without the ubiquitous sheep, the British uplands might have been as rich as alpine arctic flora as many parts of Scandinavia. Pastoralism by both sheep and cattle tends to lead to deterioration of the land, as valuable minerals, especially calcium, phosphate and nitrogen, essential to plant growth, are removed with the animals' carcases. Pastoralism is an extractive, depleting form of land use, in contrast to afforestation with broad-leaved trees and semi-permanent forms of agriculture, . . . which continually build up the fertility of

the land." Such comments are frequently combined with criticism of moor-burning, which is often undertaken in association with grazing, and both processes are considered to be major causes of erosion. The extent of erosion is commonly stressed, thus Lockie (1966) says "on some West Highland hills, man-induced erosion has reduced the potential grazing by 50 per cent or more".

In contrast those who disagree wholly or partially with these criticisms apply their comments to situations much more circumscribed. Only rarely do they venture as far as Ryder (1968) who said that the Scottish hills are not well suited for cattle, and "where pasture has deteriorated this has been due as much to under-grazing by sheep as to the lack of cattle". Many studies on particular aspects of the grazing problem in particular circumstances have now been made, and it would seem that increasing grazing by no means always leads to deterioration in botanical composition. But it is difficult as yet to produce a synthesis relating to the British uplands as a whole and spanning the time intervals appropriate for trends which may take many years to show.

The rise of grazing as an ecological factor

At the climatic optimum in the post-glacial period woodland extended at least to an altitude of 700m in much of Britain. Large herbivores such as the auroch, the red deer and wild boar lived in the forest, and must have had at least local influence on the vegetation, (cf. bison in N. American forests (McAndrews 1966)). Although the woodland would not be entirely closed, it is widely held that the vegetation was not floristically rich, but that less competitive species needing open or disturbed conditions became much restricted at this time (Godwin 1956, Dickson 1973). The first major decline of woodland came with the onset of widespread blanket bog development in the Atlantic period, a change hitherto regarded as being climatically controlled (Smith 1970). Some recent studies, however, point to the influence of Mesolithic man and his livestock being at least locally important (Moore 1973). On drier soils too there was replacement of broad-leaved woodland by ericaceous moorland, and the resulting soil impoverishment has intensified restriction of the flora (Dimbleby 1962).

The next major decline of woodland, in Bronze and Iron Age times, can be more certainly ascribed to human influence (Birks 1972, Turner 1970). Further decline in the present millenium has undoubtedly been hastened by the increasing stocking of sheep and cattle (Moore and Chater 1969, Tallis & McGuire 1972), and latterly the maintenance of artificially high numbers of deer for sporting purposes, although timber extraction (Anderson 1967) and burning have also been important. By medieval times some upland areas in Wales and northern England were already grazed sufficiently as to maintain good pasture for many years (Donkin 1962, Emery 1967, Hughes et al 1973). Occasionally these grazings are explicitly stated to be grassland (Lloyd, Grime & Rorison, 1971, Tallis & McGuire 1972); more often this is surmised. But over most of the British uplands apart from the Scottish Highlands there must have been moorland and bog with dwarf shrubs dominant, particularly heather, judging from the pollen record and the numbers of domestic livestock (Franklin 1952, Thirsk 1967), considering the impact of these animals to be

discussed in the next section. Although erosion of peat was already widespread by this time, recent workers e.g. Mayfield & Pearson (1972) do not consider grazing animals to be a major cause.

Grazing as a determinant of vegetation type

Observations on the effect of grazing were made long before ecology developed as a science. It was realised that forests would not regenerate when grazed by domestic livestock, and the Board of Agriculture surveyors at the turn of the eighteenth century well understood that heavy grazing either kept short or eliminated dwarf-shrub heath. At the start of the twentieth century workers describing and mapping upland vegetation discussed the status of the various types of acidic grassland on wet rough grazings, without displaying much understanding of the grazing factor. One of the first critical studies on grazing, made in Breckland, showed that rabbits could oust *Calluna* and produce differentiation into separate plant communities within the broad grassland type (Farrow 1917).

It is now known that heavy grazing leads to the elimination of dwarf-shrub communities over a wide range of soil and climatic conditions. On drier soils Agrosto-Festucetum is formed with species richness proportional to soil nutrient status; in rather wetter conditions Nardetum results, and on peaty gleys and blanket peats Molinietum, Juncetum squarrosi or Eriophoretum. When grazing is reduced dwarf shrubs return, although this may take a long time if they have been lost entirely from the sward. Most studies have been intuitive, making use of observations of fence-lines e.g. Tansley (1939), descriptions by former residents, comparisons of vegetation maps over periods with grazing intensity approximately known e.g. Pearsall (1941), and evidence of trend displayed by the vegetation itself e.g. Ratcliffe (1959). But the conclusions are substantiated by a small number of studies in which grazing has been experimentally manipulated and the resulting changes in botanical composition observed e.g. Jones (1967) for Agrosto-Festucetum in North Wales, and Rawes & Williams (1973) for Eriophoretum in the Pennines.

Progress in the quantification of the animal densities which bring about these changes, and the rates at which they occur, has been slow, but the present author is obtaining data for sites between sea level and 700m in N.E. Scotland. The threshold density to initiate *Calluna* decline is here very broadly 1 sheep per acre, or equivalent biomasses of cattle and deer. With higher pressures there are strong indications that change can be completed within a decade, at least in some situations. It must be stressed that these densities relate to what is actually imposed on the vegetation; they are not stocking rates which may hide the marked local variation usually occurring within large grazing units. If no other vegetation is grazed such high densities may well lead to poor herbivore performance. They do not necessarily occur by free choice by the animals, but often result from management considerations and the particular disposition of vegetation types in relation to such factors as shelter, land form and accessibility to the farm or improved grazings.

The herbivore densities which prevent woodland regeneration or establishment of trees are certainly very low, but have never been measured accurately.

The number of plants per unit area which have to be grazed is minute in comparison to the numbers involved in the successions between heath and grassland, and young trees are relatively preferred food. The degree of selectivity shown by the grazing animal, and the density, visibility and palatability of the young trees are important controlling factors (Nicholson 1970). Thus young deciduous trees like birch will be less vulnerable to grazing once their leaves have fallen than evergreens like pine, given equal palatability. Potentially then the pattern, type and extent of grazing could cause divergence in the succession to woodland, but no certain examples have been reported in the British uplands.

There is also evidence that grazing can deflect succession to dwarf-shrub heath, or vary its composition, particular rates being favourable to *Erica cinerea* (Gimingham 1949) or *Vaccinium myrtillus*. Grant & Hunter (1968) have shown experimentally that the structure and form of Callunetum depend on the grazing imposed; with lighter grazing *Calluna* grows tall sooner, which means with present policies of management that burning will be undertaken more frequently. On the other hand Welch & Kemp (1973) have described an unburnt Callunetum kept short by sheep for at least thirty years, containing as yet only a small proportion of grasses.

These variations within dwarf-shrub heath are less important in considering floristics and land-use in the British uplands than the variations in type of grassland, some of which are ascribed to grazing. Those who condemn the practice of grazing argue that unpalatable species such as *Nardus* and *Molinia* spread at the expense of 'sweeter' grasses like *Agrostis, Festuca* and *Poa*. They say this process has led to the development of large tracts of Nardetum and Molinietum from Agrosto-Festucetum. Both Pearsall (1950) and Coppock & Coleman (1970) present plates showing *Nardus* invading over-grazed Agrosto-Festucetum, without giving any indication that vegetation trend and animal usage were measured. But when heavy grazing has been experimentally imposed both *Nardus* and *Molinia* declined (Fenton 1937, Jones 1967, Nicholson et al 1970). It is possible the selectivity of the grazing animal was affected by their confinement in enclosures; nevertheless the presence in Agrosto-Festucetum of small very closely grazed plants of *Nardus,* found to be old on uprooting, does prove that this species can be controlled at least for a time under free-range grazing. In my opinion the two plates depict a transition in soil conditions, the *Nardus* growing where drainage is rather more impeded. Its morphology is such that lateral spread of the tussocks is very slow, so invasion will depend on establishment from seed, which is unlikely to produce sharp lateral variation in the numbers of tall ungrazed tussocks.

Succession from Agrosto-Festucetum to Nardetum will proceed most rapidly where drainage conditions most favour the growth of *Nardus* (King 1962), and when grazing pressure is such that the tussocks escape the close grazing given to the rest of the sward. I believe that stands of Nardetum with this origin are fairly few, and that at many such sites Nardetum would have developed directly on the loss of *Calluna* had *Nardus* been able to colonise as rapidly and effectively as *Agrostis* and *Festuca*. For the same reason successions to Juncetum squarrosi in some wet species – poor Agrosto-Festuceta are

now occurring, with circular patches of *Juncus* showing marginal vigour (Kershaw & Tallis 1958, Welch 1964). But overall only a small proportion of the total area of Agrosto-Festucetum in the British uplands is vulnerable to these changes.

The decline of *Nardus* under heavy grazing, though demonstrated experimentally, is likely to be infrequent on the hill, because the penalty in performance is so great (Floate *et al* 1973) that managers will wherever possible avoid imposing it on their livestock. Decline of *Molinia,* at least in mixed swards, can be brought about more readily (Jones 1967, Nicholson *et al* 1970), and has probably occurred locally in Wales, the Lake District and Southern Scotland, Dale (1973) having reported summer sheep densities on *Molinia* grasslands in Snowdonia as high as 1.5 per acre, considerably greater than on Nardetum. The timing of grazing is especially critical with these species because the leaves soon die, whereupon the animals will be less inclined to graze and defoliation may have less impact.

Complete or virtual removal of grazing causes other successions in grassland-type vegetation. Taller-growing grass species quickly become dominant although later dwarf-shrub heath and ultimately woodland will develop at most sites. *Juncus squarrosus* is lost within a few years, often being replaced by *Deschampsia flexuosa* (Welch & Rawes 1964). *Nardus* also has been found to decline, both when occurring scattered in a Festuca grassland (Welch & Rawes, 1964), and when dominant, Dale (1973) reporting replacement by *Molinia.* On better soils *Agrostis, Deschampsia caespitosa, Festuca rubra* and *Holcus lanatus* increase at the expense of lower-growing species such as *Thymus drucei* and *Trifolium repens* (Dale 1973, Jones 1967, Welch & Rawes 1964), and vegetation akin to the Tall Herb nodum of McVean and Ratcliffe (1962) will eventually develop, at least temporarily.

Very heavy grazing appears to encourage bryophytes at the expense of higher plants. The swards that attract such pressures are mainly those containing palatable grasses on nutrient-rich sites e.g. calcareous flushes, and species-rich Agrosto-Festucetum (Welch & Rawes 1965), but in the montane zone where growth is much reduced quite low animal densities may be sufficient.

The type of vegetation produced under grazing can depend on the species of herbivore. Cattle are known to graze more coarsely than sheep or deer, and are therefore more likely to depress unpalatable plants like *Molinia* and *Nardus* (Fenton 1937), although they do not necessarily graze more closely (Nicholson *et al* 1970). But no one has yet demonstrated this sort of differentation in Britain. My own studies suggest that the threshold biomass of cattle needed to oust *Calluna* is rather lower than of sheep, and that this is partly due to the dung having greater effects. It not only obliterates a proportion of the plants, but also provides a niche that is colonised by rapid-growing species from the periphery, and by propagules either deposited in the dung after passage through the animal or which are dispersed on to it. Smaller herbivores also have distinctive effects on the vegetation, but mountain hares cannot oust *Calluna* (Welch & Kemp 1973), unlike rabbits which produce Agrosto-Festucetum (Farrow 1917, Fenton 1940).

Grazing as a determinant of floristic richness

Inasmuch as different plant communities contain different numbers of species, the successions due to grazing described in the previous section will affect floristic richness. Furthermore the same communities may differ in mean species number per unit area under different grazing regimes, and the total richness of an area depends on the range and number of plant communities occurring.

Within small areas richness is influenced by the size of the plants. It is significant that in the British uplands bryophytic flush communities and some forms of Agrosto-Festucetum have the greatest density of species (McVean & Ratcliffe 1962). These vegetation types occur on base-rich soils, and the plants are always kept short by heavy grazing. Grime (1973) has shown that the number of species per square metre is directly related to the amount of grazing received in a wide range of grasslands in the Southern Pennines, suggesting that at this scale there is a general relationship between grazing and richness.

British upland vegetation is, however, widely regarded as improverished in species, and many authors e.g. Pearsall (1950) and Hart (1968), previously quoted, attribute this to grazing. But species may be absent from Britain because they failed to return after the last glaciation, or due to climatic limitations. The prevailing oceanicity which has resulted in our bryophyte flora being richer than in many other parts of Europe (Dickson 1973) may have adversely affected the numbers of higher plants, possibly due to temperatures being insufficiently low in winter and even in summer during the Post-glacial warm period (Conolly & Dahl 1970). And it is becoming increasingly clear from the fossil and pollen record that comparatively few species have become extinct in Britain in Post-glacial times, factors other than grazing being mainly responsible e.g. draining. So if our overall flora is poor, grazing should be absolved as a cause.

Nevertheless the most prevalent types of vegetation in the British uplands are composed of relatively few species, and higher plants with a much restricted distribution, confined to rock ledges on a few mountains, do form a considerable proportion of the total flora. Trials have shown that some at least of these species can thrive elsewhere in the absence of grazing (Rawes & Welch 1972). Stands containing such species belong to the Tall Herb nodum, but how extensive this was before the grazing of domestic livestock became prevalent is uncertain. Probably succession to woodland was only prevented in extreme conditions, caused for example by shallow soil or much exposure, and even then *Calluna* and *Vaccinium myrtillus* would attain dominance except on base-rich sites, where tall herbs and ferns could compete successfully. But related tall-growing vegetation would grow below the trees and in natural openings of the tree canopy, and many of the constituent plants of the nodum still occur in woodland. So it is reasonable to conclude that grazing by eliminating the types of plant community containing tall herbs, substantially curtails floral diversity, when this is reckoned for units as large as hillsides, and that attractive flowers have suffered most. If, however, grazing now ceased, diversity in this sense would not necessarily increase in many parts of Britain, because seed sources are lacking.

The relative importance of grazing as a factor controlling British upland vegetation.

Grazing determines what broad type of vegetation nearly all terrestrial habitats in Britain support, particular intensities resulting in the preponderance of plants belonging to the different life-form classes of Raunkiaer. Other factors are paramount only where growth is much restricted in a small number of habitats, including those at high altitude, those where snow-lie is prolonged, and those where soils are very thin or toxic (McVean & Ratcliffe 1962).

Within the broad types of vegetation climatic and edaphic factors, as well as grazing, govern the occurrence of particular species, including the dominants, so controlling the distribution of the plant communities. The actual numbers of constituent species in the communities change little along the climatic and soil moisture gradients, as shown by McVean & Ratcliffe (1962) for Scottish Highland vegetation, and by Shimwell (1971) for calcareous grassland throughout Britain. But there is a sharp increase in species number with increasing pH or soil nutrient content (Grime 1973). In comparison the effects of grazing on floristic richness discussed in the last section are not so great.

Both dwarf-shrub heath and grasslands conform to these generalisations. In the former there is some variation due to grazing, but the flora is markedly more diverse on more calcareous soils, and at the highest pH levels *Dryas* takes dominance causing a major change in structure. In grasslands grazing has greater significance, not only in creating swards with high species density, but also in governing the occurrence of species varying greatly in value as food. Although I consider some authors have exaggerated the degree and extent of adverse trends caused by grazing, nevertheless unpalatable species have increased and are continuing to increase on some soil types, a result largely attributable to the selective habit.

'Over-grazing' and 'under-grazing' as often used are far too simple terms to adequately describe the position on many British hills. It must be stressed that good management for livestock should take advantage of the seasonal variation in palatability and food value of the principal upland species, and maintain for this a variety of vegetation types. Thus heavy pressures may be needed in parts of the grazing unit, and elsewhere light pressures; in general grazing must be controlled to manage the resource for sustained production. Until means of doing this efficiently and effectively have been obtained, it would be wrong to condemn too severely free-range grazing which though providing a valuable product may cause some decline in part of the resource. Only where such trends are widespread and apparently irreversible is there immediate need of change in management.

Acknowledgements

Mr. I.A. Nicholson has made most useful comments on the drafts.

References

Anderson, M.L. (1967) A History of Scottish Forestry, Vol. I, Thomas Nelson, Edinburgh, 662 pp.

Birks, H.H. (1972) Studies in the vegetational history of Scotland. II Two pollen diagrams from the Galloway Hills, Kirkcudbrightshire. J. Ecol. *60* 183–217,

Conolly, A.P. & Dahl, E. (1970) Maximum summer temperature in relation to the modern and quaternary distributions of certain arctic-montane species in the British Isles. IN: Studies in the Vegetational History of the British Isles, ed. Walker, D. & West, R.G., pp 159–223.

Coppock, J.T. & Coleman, A.M. (1970) Land use and conservation. II The conservation of wildscape: a quest for facts. Geog. J. *136* 191–210.

Dale, J. (1973) Sheep grazing experiments in Snowdonia. Nature Wales *13* 229)234.

Darling, F.F. (1955) West Highland Survey. Oxford University Press, 438 pp.

Dickson, J.H. (1973) Bryophytes of the Pleistocene. Cambridge University Press, 256 pp.

Dimbleby, G.W. (1962) The development of British heathlands and their soils. Oxf.For.Mem. *23* 1–121.

Donkin, R.A. (1962) Cattle on the estates of medieval Cistercian monasteries in England and Wales. Econ. Hist. Rev. 2nd series, *15* 31–53.

Emery, F. (1967) The farming regions of Wales. In: The Agrarian History of England and Wales, Vol. IV 1500–1640, ed. Thirsk, J., pp 113–160.

Farrow, E.P. (1917) On the ecology of the vegetation of Breckland. III General effects of rabbits on the vegetation. J.Ecol. *5* 1–18.

Fenton, E.W. (1937) The influence of sheep on the vegetation of hill grazings in Scotland. J. Ecol. *25* 424–430.

Fenton, E.W. (1940) The influence of rabbits on the vegetation of certain hill-grazing districts in Scotland. J. Ecol. *28* 438–449.

Floate, M.J.S., Eadie, J., Black, J.S. & Nicholson, I.A. (1973) The improvement of *Nardus* dominant hill pasture by grazing control and fertilizer treatment and its economic assessment. Potassium Institute Ltd Colloquium Proc. No. 3, pp 33–39.

Franklin, T.B. (1952) A History of Scottish Farming. Thomas Nelson, London, 194pp.

Gimingham, C.H. (1949) The effects of grazing on the balance between *Erica cinerea* L. and *Calluna vulgaris* (L.) Hull in upland heath, and their morphological responses. J. Ecol. *37* 100–119.

Godwin, H. (1956) The History of the British Flora. Cambridge University Press, 384 pp.

Grant, S.A. & Hunter, R.F. (1968) Interactions of grazing and burning on heather moors and their implications in heather management. J. Br. Grassld. Soc. *23* 285–293.

Grime, J. (1973) Control of species density in herbaceous vegetation. J. envir. Mgmt. *1* 151–167.

Hart, R.A. de J. (1968) The Inviolable Hills. Stuart & Watkins, London, 244 pp.

Hughes, R.E., Dale, J., Williams, I.E. & Rees, D.I. (1973) Studies in sheep population and environment in the mountains of North-west Wales. I The status of sheep in the mountains of North Wales since medieval times. J. appl. Ecol. *10* 113–132.

Jones, L.I. (1967) Studies on hill land in Wales. Tech. Bull. Welsh Pl. Breeding Station No. 2, Aberystwyth, 179 pp.

Kershaw, K.A. & Tallis, J.H. (1958) Pattern in a high-level *Juncus squarrosus* community. J. Ecol. *46* 739–748.

King, J. (1962) The *Festuca-Agrostis* grassland complex in south-east Scotland. J. Ecol. *50* 321–355.

Lloyd, P.S., Grime, J.P. & Rorison, I.H. (1971) The grassland vegetation of the Sheffield region. I General features. J. Ecol. *59* 863–886.

Lockie, J.D. (1966) The use of red deer *(Cervus elaphus)* in Highland Scotland. 6th Congress Forestal Mundial, Madrid, June 1966, 11 pp.

McAndrews, J.H. (1966) Post-glacial history of prairies, savanna, and forest in Northwestern Minnesota. Mem. Torrey bot. Club *22* 1–72.

McVean, D.N. & Lockie, J.D. (1969) Ecology and Land Use in Upland Scotland. University Press, Edinburgh, 134 pp.

McVean, D.N. & Ratcliffe, D.A. (1962) Plant communities of the Scottish Highlands. Monographs of the Nature Conservancy No.1, London 445 pp.

Mayfield, B. & Peafson, M.C. (1972) Human interference with the north Derbyshire blanket peat. E. Midld. Geogr. *5* 245–251.

Moore, P.D. (1973) The influence of prehistoric cultures upon the initiation and spread of blanket bog in upland Wales. Nature, Lond. *241* 350–353.

Moore, P.D. & Chater, E.H. (1969) The changing vegetation of west-central Wales in the light of human history. J. Ecol. *57* 361–379.

Nicholson, I.A. (1970) Some effects of animal grazing and browsing on vegetation. Trans. bot. Soc. Edinb. *41* 85–94.

Nicholson, I.A., Paterson, I.S. & Currie, A. (1970) A study of vegetational dynamics: selection by sheep and cattle in *Nardus* pasture. In: Animal Populations in relation to their Food Resources. British Ecological Society Symposium No.10, ed. Watson, A., pp 129–143.

Pearsall, W.H. (1941) The 'mosses' of the Stainmore district. J.Ecol. *29* 161–175.

Pearsall, W.H. (1950) Mountains and moorlands. Collins, London, 312 pp.

Ratcliffe, D.A. (1959) The vegetation of the Carneddau, North Wales. I Grasslands, heaths and bogs. J. Ecol. *47* 371–413.

Rawes, M. & Welch, D. (1972) Trials to recreate floristically-rich vegetation by plant introduction in the northern Pennines. England. Biol. Cons. *4* 135–140.

Rawes, M. & Williams, R. (1973) Production and utilisation of *Calluna* and *Eriophorum*. Potassium Institute Ltd Colloquium Proc. No. 3, pp 115–119

Ryder, M.L. (1968) Sheep and the clearances in the Scottish Highlands: a biologist's view. Agric. Hist. Review *16* 155–158.

Shimwell, D.W. (1971) Festuco-Brometea Br.–Bl. & R. Tx. 1943 in the British Isles: the phytogeography and phytosociology of limestone grasslands. Parts I and II. Vegetatio *23* 1–60.

Smith, A.G. (1970) The influence of Mesolithic and Neolithic man on British vegetation: a discussion. In: Studies in the Vegetational History of the British Isles, ed. Walker, D. & West, R.G., pp 81–96.

Tallis, J.H. & McGuire, J. (1972) Central Rossendale: the evolution of an upland vegetation. I Clearance of woodland. J. Ecol. *60* 721–737.

Tansley, A.G. (1939) The British Islands and their Vegetation. Cambridge University Press.

Thirsk, J. (1967) The Agrarian History of England and Wales. IV 1500–1640, Cambridge University Press, 919 pp.

Tivy, J. (1973) The Organic Resources of Scotland. Oliver & Boyd, Edinburgh, 227 pp.

Turner, J. (1970) Post-neolithic disturbance of British vegetation. In: Studies in the Vegetational History of the British Isles, ed. Walker, D. & West, R.G., pp 97–116.

Welch, D. (1964) Studies in the autecology of *Juncus squarrosus* L. M. Sc. thesis, University of Durham.

Welch, D. (1969) Sheep grazing in northern England: some ecological consideration. In: Hill-land productivity. Occ. Symp. Br. Grassld. Soc. No. 4, ed. Hunt, I.V., pp 149–155.

Welch, D. & Kemp, E. (1973) A Callunetum subjected to intensive grazing by mountain hares. Trans. bot. Soc. Edinb. *42* 89–99.

Welch, D. & Rawes, M. (1964) The early effects of excluding sheep from high-level grasslands in the north Pennines. J. appl. Ecol. *1* 281–300.

Welch, D. & Rawes, M. (1965) The herbage production of some Pennine grasslands Oikos *16* 39–47.